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Assessing components of competition indices for young boreal plantations

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MACDONALD, G. B., MORRIS, D. M., and MARSHALL, P. L. 1990. Assessing components of competition indices for young boreal plantations. Can. J. For. Res. **20**: 1060–1068.

Important components of interspecific competition affecting apical and cambial growth in young plantations of black spruce (*Picea mariana* (Mill.) B.S.P.) and jack pine (*Pinus banksiana* Lamb.) in northern Ontario were identified. The relative importance of competition, initial seedling status, and some soil factors was also assessed. Measures of perennial competition were calculated using hemispherical photographs, stand maps, and mensurational data from 360 seedling-centred plots (1.4 m radius) for each of the two species. Fractal geometry was used to quantify the textures of the competing canopies. Reliable competition indices should include horizontal and vertical dimensions and express the amount of competition relative to the size of the seedling. The total canopy fraction on the photographs and some simple field measurements of competition correlated significantly with seedling growth. Complex expressions of competition were unjustified, and measures of dispersion and canopy texture correlated weakly with growth. The consistently good correlations between growth and some components of competition revealed that an index applicable to all species, stock types, and growth responses could be developed.

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D'importantes composantes de la compétition interspécifique qui influencent la croissance en diamètre et en hauteur dans les jeunes plantations d'Épinette noire (*Picea mariana* (Mill.) B.S.P.) et de Pin gris (*Pinus banksiana* Lamb.) dans le nord de l'Ontario ont été identifiées. L'importance relative de la compétition, de l'état initial des semis et de quelques caractéristiques du sol a été évaluée. Des valeurs de compétition par la végétation pérenne ont été calculées à partir de photographies hémisphériques, de cartes de peuplement et de données dendrométriques provenant de 360 placettes échantillons circulaires (1,4 m de rayon) avec un semis comme centre, pour chacune des deux espèces. La géométrie des fractals a été utilisée pour quantifier la texture du couvert végétal compétiteur. Des indices fiables de compétition devraient inclure des dimensions horizontales et verticales et exprimer l'intensité de la compétition relativement à la dimension des semis. La fraction du couvert total sur les photographies et quelques mesures simples de la compétition sur le terrain étaient corrélées significativement avec la croissance des semis. Des expressions complexes de la compétition n'étaient pas justifiées et les mesures de dispersion et de texture du couvert étaient faiblement corrélées avec la croissance. L'obtention constante de bonnes corrélations entre la croissance et quelques composantes de la compétition montre qu'un indice applicable à toutes les espèces, les types de semis et les réponses de croissance pourrait être développé.

[Traduit par la revue]

Introduction

Interspecific competition is a serious threat to plantation performance across North America (Eis 1981; Oxenham 1983; Knapp *et al.* 1984; Oliver 1984; Fox 1986). The backlog of suppressed plantations is large, but all regenerated areas cannot be weeded because treatment costs are prohibitive and public resistance to the application of herbicides is increasing. Thus, reliable methods for assessing competitive effects are required to rank plantations for urgency of tending.

Ineffective assessment of competition can result in considerable economic loss when release treatments are either delayed or applied in nonthreatening situations (Weingartner and Basham 1979). Early identification of competition problems is essential because growth losses are not recoverable, replanting is expensive, and late control of advanced competition is difficult (Tappeiner and Wagner 1987).

Indices used for measuring competitive pressure on individual trees are commonly based on the relative diameters of subject and competitors and on the horizontal proximity of neighbours. Formulations range from simple "nearest neighbour" calculations (Cottam and Curtis 1956) and size-distance combinations (Mack and Harper 1977; Lorimer 1983) to complex indices using influence zone overlap (Gerrard 1969; Bella 1971; Keister 1971) or ground area potentially available to individual trees (Mead 1966; Moore *et al.* 1973).

Some indices consider competitor dispersion (Mack and Harper 1977), the degree of overtopping by competitors (Ford and Diggle 1981; Cannell *et al.* 1984), or a combination of the horizontal and vertical dimensions of competition (Howard and Newton 1984; Brand 1986). Radiometric approaches have been used to directly assess the effect of

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light obscuration (Waring 1983; Lang 1987), and hemispherical photographs have provided aboveground competition estimates (Anderson 1971; Lakso 1980; Chan and Walstad 1987).

Most existing indices were developed to assess intraspecific competition for improving growth predictions in mature stands. Testing and possibly reformulating these indices are required to explain competitive mechanisms and to quantify interspecific competition in young plantations.

This study addressed the effects of interspecific competition from perennials on the performance of individual black spruce (*Picea mariana* (Mill.) B.S.P.) and jack pine (*Pinus banksiana* Lamb.) seedlings in northern Ontario. Perennial competitors threaten plantation productivity on upland sites, which can be completely dominated by suckers of trembling aspen (*Populus tremuloides* Michx.) soon after disturbance (Pollard 1971). The subject species were chosen because of their dominant commercial status and the lack of information regarding their response to competition. Both container and bare-root stock were considered because differences in physiological responses to soil-moisture conditions exist between the two types in the first growing season (Blake and Sutton 1987), and the effects of these differences may persist. The study objectives were (1) to examine the importance to seedling growth of vertical and horizontal competition level, competitor distribution pattern, seedling size, seedling nitrogen status, and soil factors and (2) to recommend the appropriate components of an index for assessing the effects of competition on the growth of young boreal plantations.

Methods

Field and laboratory

Six black spruce plantations entering their fourth field growing season were selected during 1987. Three of the plantations originated as overwintered paper-pot container stock; the other three, as 1 1/2 + 1 1/2 bare-root stock. The plantations were on upland soils ranging in texture from coarse sand to clay. They were located between 48°32′N and 49°53′N latitude and between 85°10′W and 90°39′W longitude. Six jack pine plantations entering their fourth field growing season were sampled during 1988. Three of the plantations were overwintered paper-pot container stock, and the remaining three were 2 + 0 bare-root stock. The soils ranged from loamy sand to silty clay. The plantations were situated between 48°33′N and 49°36′N latitude and between 90°09′W and 92°15′W longitude.

Sixty seedlings were chosen in each plantation by establishing a 4 × 4 m grid, randomly selecting 60 points of intersection of the grid lines, and sampling the seedling closest to each point. Selected seedlings were replaced with new random samples if they displayed damage unrelated to competition pressure. As the seedlings were planted at a 2-m spacing and were to have a 1.4 m competition radius, the sampling method avoided overlapping of adjacent plots.

A plot radius of 1.4 m was selected to give an average sample size of 20 competitors around each seedling. This was based on preliminary counts averaging 35 000 stems/ha of perennial competitors in the selected plantations. It was judged that 20 neighbouring trees would contribute most of the competitive effect. Constraints on sampling resources dictated that an increase in the number of competitors measured would have necessitated an undesirable reduction in the number of plots.

Field measurements were conducted between mid-July and mid-September, after most of the height growth and foliage development had been completed for the seedlings and competitors. A 300-g soil sample was taken from the upper B horizon near the base of each seedling sampled. The percent ground cover of herbaceous vegetation was estimated to a 1.4 m radius around each seedling. A vertical hemispherical photograph was obtained using a 7.5-mm equidistant fish-eye lens levelled with the camera focal plane at the base of the seedling's leader. A range pole placed due east of the seedling provided directional reference in each photograph.

The following variables were measured for all perennial competitors within a 1.4 m radius of the seedling: (1) species; (2) distance to seedling; (3) azimuth from seedling; (4) total height; (5) crown length; (6) crown width; and (7) root collar diameter.

The seedlings were destructively sampled following bud set. Needles were removed for nutrient analysis and for fresh leaf area determination from the uppermost lateral branches, using 200 needles per seedling for black spruce and 100 needles per seedling for jack pine. The total height and current height increment were recorded. Current shoots were clipped, and a basal disk was removed for ring analysis.

In the laboratory the soil samples were air dried, sieved (2 mm), and analyzed for pH, clay fraction (Bouyoucos hydrometer method), and total nitrogen (macro-Kjeldahl procedure). The clay fraction was favoured as a measure of soil texture because it relates well to cation exchange capacity and moisture availability (Black 1968; Goldberg 1987). The projected areas of the fresh needle samples were measured with a Li-Cor 3100 area meter. The ovendry masses of the needle samples were later determined (drying for 48 hours at 70°C), and total nitrogen analyses were conducted. Ovendry masses of the remaining foliage were determined, and the seedling leaf area was calculated by multiplying the total ovendry mass of current foliage by the ratio of leaf area to dry mass from the needle subsample. Current increments were measured on two radii of each basal disk.

The opaque and transparent canopy areas on each hemispherical photograph were planimetered and converted to canopy fractions to provide unweighted measures of diffuse radiation interference. Automated measurement systems based on the opacity of the corresponding negatives are available (Chan *et al.* 1986). However, a manual system was used to prevent interpretation errors, such as the classification of sunlit foliage as open sky.

The view factor was used as an alternate measure of diffuse radiation interference to correct for the radiation incidence angle. Each circular hemispherical photograph was divided into three annuli, and the canopy fraction (Fi) of each annulus was estimated using an overlay to divide the annulus into segments of equal area. The sky view factor formula of Kelliher (1985) was modified to give the canopy view factor (VIEW);

$$[1] \quad \text{VIEW} = (\pi/n) \sum (\text{Fi})\cos[(\text{Ri}/\text{Ro})(\pi/2)]\sin[(\text{Ri}/\text{Ro})(\pi/2)]$$

where n is the number of annuli (3 in this case), Ri is the linear distance on the photograph from the zenith to the midpoint of the i^{th} annulus, and Ro is the distance on the photograph from the zenith to the horizon.

The maximum solar-path bandwidth for the growing season was calculated from the elevation and azimuth of the sun at each hour on the extremities (June 22 and August 22), using the formulae in Anderson (1971). Following adjustment of magnetic north to true north (Department of Energy, Mines, and Resources 1980), the solar path was outlined on a transparent overlay and divided into 16 segments of equal area to facilitate the estimation of canopy fraction. The fraction in each segment was weighted for the solar elevation angle (θ) at its midpoint, using $\sin\theta$ in accordance with Lambert's Law (Campbell 1977). The weighted average of the canopy fractions was used as the measure of direct radiation interference.

Indices of horizontal competition based on field measurements included competitor density, sum of competitor root collar basal area, and sum of competitor crown volume. The latter two measures were applied both unweighted and weighted by the

TABLE 1. Descriptions and abbreviations for measures of competition, seedling status, and soil factors

Factors	Variables measured	Abbreviations
Competition	Total canopy fraction on photographs	CAN
	Opaque canopy fraction on photographs	CANO
	Transparent canopy fraction on photographs	CANT
	View factor for canopy on photographs	VIEW
	Solar-path canopy fraction on photographs	SOLAR
	Canopy fractal dimension on photographs	*D*
	Density	DENS
	Basal area sum	BAC
	Distance-weighted basal area	BACD
	Crown volume sum	CVC
	Distance-weighted crown volume	CVCD
	Angular dispersion	DISP
	Average height	HTC
	Angle sum from base of seedling	ANG
	Percent herbaceous ground cover	HERB
Seedling	Initial basal area	BAS
	Initial height	HTS
	Initial stem volume	VOLS
	Current leaf area	LAS
	Foliar nitrogen concentration	NFOL
Soil	B horizon clay fraction	CLAY
	B horizon pH	pH
	B horizon nitrogen concentration	NSOIL

reciprocals of the distances between seedling and competitor stem centres. Crown volumes were calculated assuming prolate spheroidal forms (Beyer 1987) for the crowns of the predominantly deciduous tree and shrub species. Indices of vertical competition included the average height of competitors in the plot, and the sum of the angles from the base of the seedling to the apices of the competitors.

The distribution of competing stems was quantified by the formula for angular dispersion (DISP), applied to annuals by Mack and Harper (1977):

$$[2] \quad \text{DISP} = \{[(\sum \sin \theta i)/n]^2 + [(\sum \cos \theta i)/n]^2\}^{1/2}$$

where θi is the azimuth to the ith competitor, and n is the number of competitors. The value of DISP increases from 0 to 1 as competitors vary from completely dispersed to regularly clumped.

Canopy texture was assessed by the fractal dimension (D) of the foliage on the hemispherical photographs for all black spruce plantations. Mandelbrot (1967, 1982) proposed the term "fractal dimension" to describe the degree of roughness of curves. The fractal dimension is calculated as follows (Mandelbrot 1967):

$$[3] \quad LG = MG^{1-D}$$

where L is the number of scale lengths contained by the curve, G is the length of scale chosen, M is a positive constant, and D is the fractal dimension. As D rises from 1 to 2, the increasing roughness of the curve causes it to change from a straight line to total coverage of the available two-dimensional space. Classical scaling concepts do not account for irregular structures that defy the required assumptions of continuity and homogeneity (West and Goldberger 1987). Thus, fractal geometry has good potential for application in biological systems, most of which are highly irregular.

Twelve equally spaced radii on each hemispherical photograph were used as sample transects. Several estimates of total transect length contained by the canopy were made on each photograph, using progressively smaller scale sizes. The number of fully contained scales or "steps" was counted, and D was calculated in each case by least squares regression following log linearization of eq. 3. Preliminary graphical analyses indicated that curve self-similarity was restricted to less than one order of magnitude in scale length. Thus, the analysis covered only the range of self-similarity common to all species and stock types, using scale lengths of 2.5, 4.0, and 6.0 mm.

All the measures of competition, seedling status, and soil are summarized in Table 1, with corresponding abbreviations.

Statistical analyses

The Pearson product–moment correlation coefficient in simple correlation analysis was used to test the degree of association between seedling growth and variables in each of three categories: competition level, seedling status, and soil quality. The most significant variable for each category was identified in the simple correlation analysis. These variables and all interactions between them were included in a multiple correlation analysis to rate the importance of each factor. A model including all variables in Table 1 with their interactions would be excessively large and would contain many autocorrelated and biologically meaningless terms. The simpler model was adequate to rate the importance of the main factors and their interactions, for guiding future index formulation and application.

Multiple correlation analysis was more appropriate than multiple regression analysis, because none of the variables had fixed values and the intention was to test associations for explanatory purposes rather than to develop a prediction equation (Dowdy and Wearden 1983). The full model was retained rather than applying one of the standard variable selection or elimination techniques. This ensured that the relative contribution of every factor could be rated in the presence of the other measured factors influencing growth. The simple and multiple correlation analyses were applied separately for each species, stock type, and response variable, using SAS statistical software (SAS Institute Inc. 1988).

Results and discussion

Examination of Figs. 1 and 2 reveals the value of considering several alternate formulations of competition intensity. The variables CAN and VIEW suggest similar competition

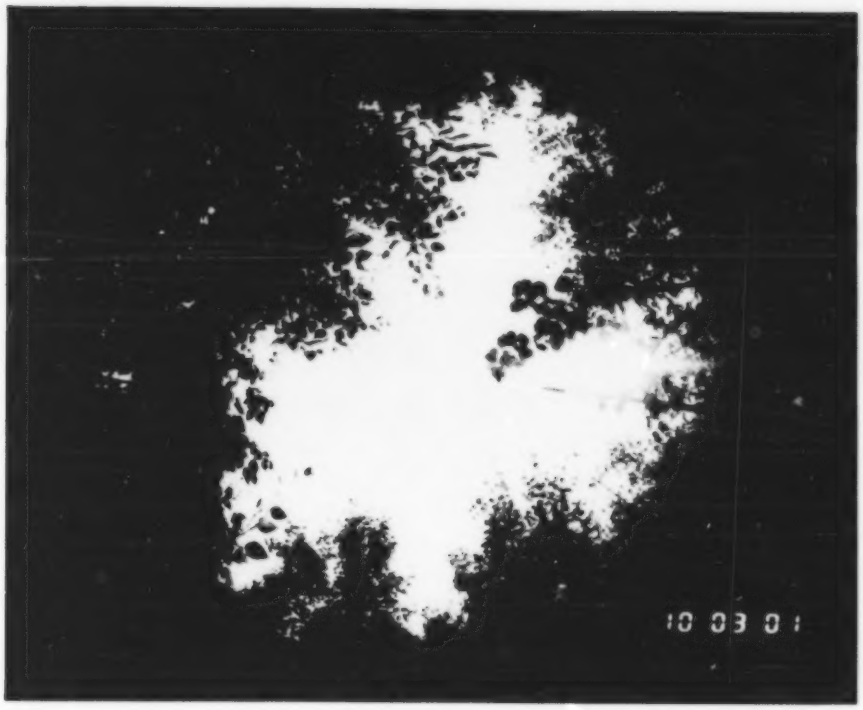

FIG. 1. Hemispherical photograph of a fine-textured canopy in a black spruce container stock plantation. The values of the derived competition measures are D = 1.148, CAN = 0.784, CANO = 0.572, CANT = 0.212, VIEW = 0.503, and SOLAR = 0.566.

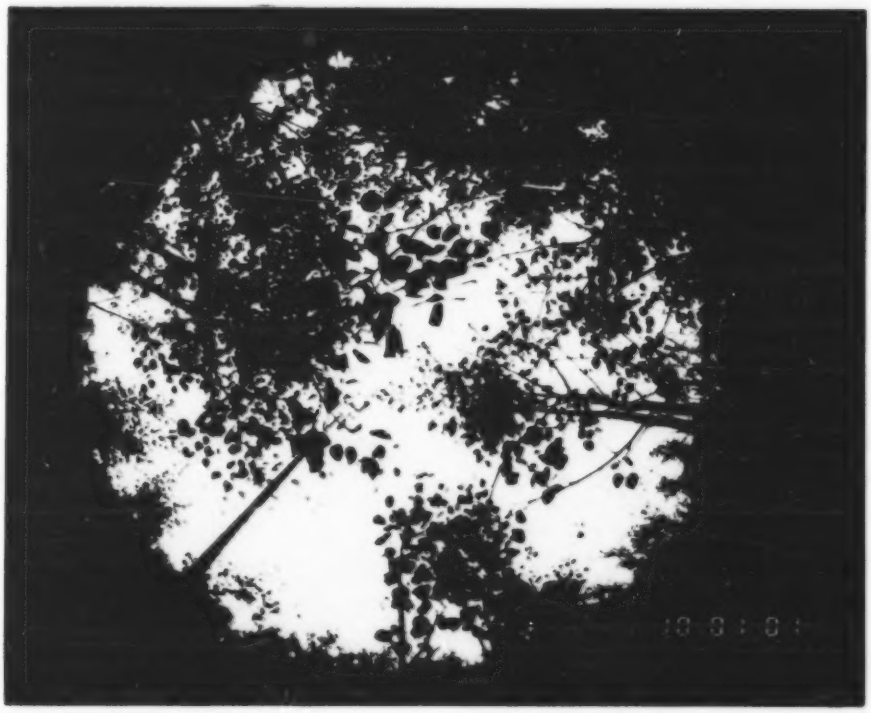

FIG. 2. Hemispherical photograph of a coarse-textured canopy in a black spruce container stock plantation. The values of the derived competition measures are D = 1.853, CAN = 0.849, CANO = 0.381, CANT = 0.468, VIEW = 0.442, and SOLAR = 0.272.

TABLE 2. Correlation coefficients for black spruce growth in association with competition, seedling, and soil measures

Measure	Container stock[a]		Bare-root stock[b]	
	Height increment[c]	Diameter increment[d]	Height increment	Diameter increment
CAN	−0.20	−0.43	$-0.06_{(0.46)}$	$-0.18_{(0.02)}$
CANO	$-0.17_{(0.03)}$	−0.37	$-0.01_{(0.86)}$	−0.19
CANT	$-0.13_{(0.09)}$	−0.27	$-0.09_{(0.21)}$	$-0.10_{(0.20)}$
VIEW	$-0.15_{(0.05)}$	−0.36	$-0.06_{(0.46)}$	$-0.17_{(0.02)}$
SOLAR	$-0.13_{(0.09)}$	−0.37	$-0.05_{(0.51)}$	$-0.16_{(0.03)}$
D	$0.05_{(0.48)}$	$0.04_{(0.57)}$	$0.02_{(0.77)}$	0.19
DENS	$-0.18_{(0.02)}$	−0.32	$-0.05_{(0.55)}$	−0.25
BAC	$-0.13_{(0.10)}$	−0.31	$0.01_{(0.89)}$	$-0.11_{(0.14)}$
BACD	$-0.09_{(0.26)}$	−0.28	$0.02_{(0.75)}$	$-0.01_{(0.86)}$
CVC	$-0.13_{(0.08)}$	−0.28	$0.04_{(0.61)}$	$0.00_{(0.99)}$
CVCD	$-0.08_{(0.28)}$	−0.22	$0.02_{(0.82)}$	$0.06_{(0.43)}$
DISP	$0.12_{(0.12)}$	$0.18_{(0.02)}$	$-0.08_{(0.28)}$	$0.08_{(0.29)}$
HTC	$0.03_{(0.71)}$	$-0.15_{(0.05)}$	$-0.01_{(0.99)}$	$-0.06_{(0.44)}$
ANG	$-0.16_{(0.04)}$	−0.34	$0.03_{(0.72)}$	−0.21
HERB	−0.32	−0.26	$-0.08_{(0.27)}$	−0.19
BAS	0.73	0.74	0.46	0.52
HTS	0.68	0.71	0.40	0.45
VOLS	0.71	0.71	0.49	0.58
LAS	0.59	0.67	0.56	0.54
NFOL	0.41	0.33	$0.09_{(0.22)}$	0.23
CLAY	−0.42	−0.38	$-0.14_{(0.06)}$	−0.35
pH	−0.36	−0.36	$-0.10_{(0.17)}$	$-0.05_{(0.51)}$
NSOIL	−0.28	−0.23	−0.21	−0.28

NOTE: *r* values are subscripted by significance levels that exceed 0.01.
[a]Sample size is 174.
[b]Sample size is 177.
[c]Current height increment.
[d]Current root collar diameter increment.

TABLE 3. Correlation coefficients for jack pine growth in association with competition, seedling, and soil measures

Measure	Container stock[a]		Bare-root stock[b]	
	Height increment[c]	Diameter increment[d]	Height increment	Diameter increment
CAN	−0.57	−0.64	−0.42	−0.78
CANO	−0.56	−0.63	−0.43	−0.78
CANT	−0.35	−0.36	−0.28	−0.57
VIEW	−0.53	−0.58	−0.42	−0.77
SOLAR	−0.49	−0.52	−0.43	−0.73
DENS	−0.24	−0.45	−0.33	−0.52
BAC	−0.36	−0.46	−0.35	−0.68
BACD	−0.38	−0.47	−0.32	−0.64
CVC	$-0.18_{(0.02)}$	−0.30	−0.24	−0.49
CVCD	$-0.15_{(0.04)}$	−0.25	−0.23	−0.47
DISP	0.25	0.34	$0.06_{(0.44)}$	0.19
HTC	−0.32	−0.28	−0.20	−0.54
ANG	−0.32	−0.49	−0.37	−0.61
HERB	−0.41	−0.26	$-0.10_{(0.20)}$	$-0.12_{(0.12)}$
BAS	0.57	0.57	0.43	0.56
HTS	0.45	0.59	$0.11_{(0.15)}$	0.42
VOLS	0.62	0.72	0.44	0.72
LAS	0.72	0.81	0.41	0.72
NFOL	$0.13_{(0.08)}$	$-0.01_{(0.92)}$	$-0.02_{(0.80)}$	−0.23
CLAY	−0.43	−0.29	$-0.14_{(0.07)}$	$-0.14_{(0.07)}$
pH	0.35	0.24	$-0.09_{(0.24)}$	$0.10_{(0.19)}$
NSOIL	$0.03_{(0.74)}$	$0.04_{(0.63)}$	$-0.18_{(0.02)}$	$-0.18_{(0.02)}$

NOTE: *r* values are subscripted by significance levels that exceed 0.01.
[a]Sample size is 177.
[b]Sample size is 176.
[c]Current height increment.
[d]Current root collar diameter increment.

levels for the two plots, whereas SOLAR indicates higher competition in Fig. 1. The fractal dimensions are effective for quantifying the canopy textures, and a higher dimension is associated with a higher fraction of transparent canopy (CANT). Clearly, no single variable is sufficient to express the various aspects of competition, such as diffuse radiation interference, direct radiation interference, and foliage texture.

Measures of radiation interception derived from hemispherical photographs were generally more effective than the measures of competition obtained from field measurements (Tables 2 and 3). The variables BAC, BACD, CVC, CVCD, HTC, and ANG required time-consuming field measurements of every competitor within the plot and extensive subsequent calculations. However, they rarely produced stronger growth correlations than the variables derived from the photographs. The photographic approach most closely approximated the perspective of the seedling, recording competitors beyond the plot radius and automatically assigning the appropriate weighting factor to competitors that were distant or partially blocked by intervening competitors. Based on its high correlations with growth for all species and stock types, CAN was selected to represent the competitive effect in the multiple correlation analysis.

The geometrical bias that can cause a strong correlation between tree size and growth rate was removed in this study by considering only specific increments as response variables (Duff and Nolan 1957). Thus, the higher correlations of the photographic measures resulted from their good expressions of the respective abilities of the seedling and competitors to capture adequate environmental resources.

Total canopy fraction (CAN) produced stronger growth correlations than the other photographic measures. The weaker negative growth correlations for the transparent fraction (CANT) compared with the opaque fraction (CANO) may be attributed to the wide range in radiation interference associated with transparent canopies. The view factor (VIEW) was nearly as effective as CAN and may be preferable in practice because its total measurement time per photograph (2.4 min) averaged less than half that of CAN.

CAN and VIEW generally produced stronger negative growth correlations than SOLAR, indicating that some reduction in direct radiation by neighbouring trees may favour growth by protecting seedlings against harmful extremes of microclimate. For example, large sunflecks were shown to increase the energy load on seedlings of red fir (*Abies magnifica* A. Murr.) without corresponding increases in carbon gain (Ustin *et al.* 1984).

Unlike CAN, VIEW and SOLAR required corrections for the angle of incident radiation. Such corrections may be detrimental in a competition index if seedlings respond similarly to radiation from all incident angles. This may partly explain why VIEW and SOLAR had slightly weaker growth correlations than CAN (see Tables 2 and 3; note particularly the container stock of each species).

The fractal dimension (D) was significantly ($p < 0.01$) correlated with diameter growth in black spruce bare-root stock (Table 2). The positive sign of the correlation indicates

TABLE 4. Importance ranking by multiple correlation analysis of competition, seedling size, soil texture, and interactions for black spruce growth

Term	Container stock[a]		Bare-root stock[b]	
	Height increment[c]	Diameter increment[d]	Height increment	Diameter increment
CAN	$-0.45_{(0.65)}$	$-2.11_{(0.04)}$	$-0.29_{(0.77)}$	$-1.77_{(0.08)}$
VOLS	$0.85_{(0.40)}$	$1.84_{(0.07)}$	$1.01_{(0.31)}$	$1.76_{(0.08)}$
CLAY	$-0.93_{(0.35)}$	$-1.39_{(0.17)}$	$0.75_{(0.45)}$	$-1.37_{(0.17)}$
CAN × VOLS	$-0.33_{(0.74)}$	$-1.65_{(0.10)}$	$0.79_{(0.43)}$	$-0.13_{(0.90)}$
CAN × CLAY	$0.28_{(0.78)}$	$0.52_{(0.60)}$	$-0.71_{(0.48)}$	$0.41_{(0.68)}$
VOLS × CLAY	$-0.02_{(0.98)}$	$-1.14_{(0.26)}$	$-0.88_{(0.38)}$	$-0.66_{(0.51)}$
CAN × VOLS × CLAY	$0.43_{(0.67)}$	$1.86_{(0.06)}$	$0.53_{(0.59)}$	$1.00_{(0.32)}$

NOTE: t values are subscripted by significance levels.
[a]Sample size is 174.
[b]Sample size is 177.
[c]Current height increment.
[d]Current root collar diameter increment.

TABLE 5. Importance ranking by multiple correlation analysis of competition, seedling size, soil texture, and interactions for jack pine growth

Term	Container stock[a]		Bare-root stock[b]	
	Height increment[c]	Diameter increment[d]	Height increment	Diameter increment
CAN	$-2.43_{(0.02)}$	$-1.96_{(0.05)}$	$-1.61_{(0.11)}$	$-1.87_{(0.06)}$
VOLS	$-0.72_{(0.47)}$	$1.57_{(0.12)}$	$-0.52_{(0.60)}$	$1.41_{(0.16)}$
CLAY	$-1.04_{(0.30)}$	$-0.27_{(0.79)}$	$-0.92_{(0.36)}$	$-0.01_{(0.99)}$
CAN × VOLS	$2.27_{(0.02)}$	$-0.16_{(0.87)}$	$0.82_{(0.41)}$	$-0.21_{(0.84)}$
CAN × CLAY	$0.60_{(0.55)}$	$0.11_{(0.91)}$	$0.63_{(0.53)}$	$-0.11_{(0.91)}$
VOLS × CLAY	$0.62_{(0.54)}$	$-0.75_{(0.45)}$	$0.20_{(0.84)}$	$-1.09_{(0.28)}$
CAN × VOLS × CLAY	$-0.89_{(0.38)}$	$0.79_{(0.43)}$	$0.15_{(0.88)}$	$0.80_{(0.43)}$

NOTE: t values are subscripted by significance levels.
[a]Sample size is 177.
[b]Sample size is 176.
[c]Current height increment.
[d]Current root collar diameter increment.

that cambial growth may be favoured by coarse, transparent canopies, which permit longer sunfleck durations than fine canopies. The insignificant growth correlations in the other cases may be attributable to counteracting positive effects of fine-textured canopies. For example, fine canopies would have more pronounced solar penumbrae than coarse canopies. Penumbrae reduce the heat and water stress per unit of photosynthetically active radiation (Anderson and Miller 1974).

Fractal geometry could be considered for quantifying seedling responses such as crown or root expansion, which may not strictly follow the principles of traditional Euclidean geometry. However, more efficient methods of obtaining the raw data for the calculations must be developed. The average time requirement for measuring canopy fractal dimension on a photograph was 6 min.

A simple stem count (DENS) provided stronger negative growth correlations than competing basal area sum (BAC, BACD) or crown volume sum (CVC, CVCD) for black spruce (Table 2) and stronger correlations than crown volume sum for jack pine (Table 3). Weighting basal area and crown volume by the distance to the subject seedling seldom improved correlations and in most cases weakened them. This suggests that time-consuming distance measurements may be omitted when assessing competition on fixed-area plots in young plantations. Previous studies (Daniels 1976; Lorimer 1983) have also found that complex measures are largely unjustified.

Among the measures of horizonal competition, growth correlations were best with competitor density (DENS) for black spruce (Table 2) and with competing basal area (BAC or BACD) for jack pine (Table 3). The weaker correlations for competing crown volumes (CVC and CVCD) may be partly explained by deviations of some of the crowns from the assumed spheroidal forms. Improved results could likely be obtained by using the more time-consuming measurement of competing leaf area.

Angular dispersion (DISP) correlated significantly with jack pine growth in most cases (Table 3), suggesting that the mutual interference among competitors in clumped patterns may benefit seedling growth for this species. Clumping may also result in less light interception per unit of competition. However, dispersion was less important than other components of competition (Tables 2 and 3). Weiner (1984) reported that the dispersion pattern of neighbours within 2 m made no significant contribution to the variation in

growth of young *Pinus rigida* Mill. trees. It is likely that distribution pattern is least important in dense young stands where a few close competitors can overtop and suppress a seedling irrespective of their angular dispersion.

The vertical angle sum of competitors (ANG) was consistently superior to average competitor height (HTC) as a measure of vertical competition. This probably resulted because HTC failed to account for the effect of competitor density. Correlations for ANG were similar to those for the significant measures of horizontal competition, indicating that both the vertical and the horizontal dimensions of competition are important.

Herbaceous vegetation cover (HERB) was not a significant factor for growth of bare-root stock of either species. Higher negative growth correlations for container stock indicated that resource interception by low vegetation may be more important for smaller seedling stock.

Seedling status expressed as basal area, volume, or leaf area correlated strongly with growth for all species and stock types. Seedling height and foliar nitrogen concentration produced weaker correlations, especially for jack pine (Table 3). The insensitivity of growth to nitrogen concentration suggests that nitrogen would be less important than radiation as a limiting resource on the sites sampled. VOLS produced consistently good growth correlations, and was therefore selected as the seedling status variable for the multiple correlation analyses.

Soil factors were less significant as a group than competition or seedling status factors. However, some significant negative correlations occurred between growth and clay fraction or soil nitrogen concentration. These results may be attributable to proportionally larger benefits to competitors than to seedlings on sites with high moisture and nutrient retention. The clay fraction (CLAY) was selected for inclusion in the multiple correlation analysis because it generally correlated more strongly than the other soil factors with seedling growth.

Jack pine growth correlated more strongly than black spruce growth with most of the competition measures. Jack pine is intolerant of shade (Fowells 1965), and radiation may be a critical factor in young plantations of this species. Weaker correlations for black spruce indicated that radiation interception may be less critical to growth in this shade-tolerant species.

With few exceptions, correlations between growth and the measures of competition, seedling status, or soil quality were higher for container stock than for bare-root stock of both species. A full explanation of these differences would require additional data enabling a comparison of the physiological conditions between the two stock types. However, it may be hypothesized that the effects of initial size advantages in bare-root stock have persisted to the fourth growing season.

Diameter increment was more highly correlated than height increment with most competition measures for both species. Xylem production tends to be more sensitive than height growth to suppression (Bormann 1965), and this general phenomenon can be explained in terms of the relative sink strengths of the corresponding meristems. The apical meristem is a strong sink, which makes its carbohydrate demand early in the growing season when stored carbohydrate is at a peak (Lanner 1985). The duration of shoot elongation is controlled by endogenous factors more than by environmental conditions (Lavender 1981). Thus, a shoot can obtain the necessary energy and growth hormones for full extension even under heavy competition. While apical growth uses both current photosynthate and carbohydrate stored in adjacent old foliage (Kozlowski and Winget 1964), the more diffuse cambial sink relies on current photosynthate alone (Lanner 1985). If seedling height is the preferred growth criterion, then one of the measures that correlates well with height growth should be included in a competition index. HERB correlated well with height growth for container stock of both species, implying that herbaceous vegetation may interfere with belowground resource acquisition in stock with small root systems.

When competition level (CAN), seedling status (VOLS), and soil texture (CLAY) were each tested in the presence of the others, competition level was generally the most significant factor (Tables 4 and 5). CAN had a higher significance level than the other two factors in five of the eight cases. Seedling size was most important in one case (height increment of black spruce bare-root stock), and as important as competition level in another case (diameter increment of black spruce bare-root stock). Soil texture was the most significant factor only for height increment of black spruce container stock. The multiple correlation analyses generally confirmed the previous results that sensitivity to competition is greater for jack pine than for black spruce, greater for container stock than for bare-root stock, and greater for diameter growth than for height growth (Tables 4 and 5).

Many previously published indices required the inclusion of subject tree size to produce acceptable growth correlations (Bella 1971; Daniels 1976; Alemdag 1978; Lorimer 1983; Brand 1986). The results for diameter growth (Tables 4 and 5) support the incorporation of seedling size into competition indices.

In general, interactions between the factors tested were not important (Tables 4 and 5). In no case was an interaction term more significant than a main factor. In the two cases where interactions were important (diameter increment of black spruce container stock and height increment of jack pine container stock), the term involved an interaction between competition level and seedling size. This reinforces the above suggestion that the size of the subject tree should be included in a competition index.

Conclusions

A broadly applicable competition index may be attainable because the relative significance of the various aspects of competition is similar for all the species – stock type – growth response combinations examined (Tables 2 and 3). Furthermore, soil texture does not appear to significantly affect the relationship between growth and competition level (Tables 4 and 5). However, growth–competition relationships are stronger for jack pine, container stock, and diameter growth than for black spruce, bare-root stock, and height growth, respectively.

A reliable index of competition in young boreal plantations should include the horizontal and vertical dimensions of competitive interactions, and should express the amount of competition relative to the size of the seedling. The level of competition appears to be more important than the competitor distribution pattern in young plantations. Simple, unweighted components are recommended for competition

indices designed to predict seedling growth rather than to explain the mechanisms of competitive effects.

The total canopy fraction on hemispherical photographs (CAN) satisfies the above requirements and can be rapidly obtained. The canopy view factor (VIEW) correlates nearly as strongly with growth and requires less time for measurement of the photographs. The canopy fractal dimension (D) derived from hemispherical photographs can be used to quantify texture of the competing canopy, but texture correlates weakly with seedling growth.

In practice, a fish-eye lens may be unavailable or the time required for film processing may be operationally unacceptable. In this case, alternate measurements such as competing basal area, vertical angle, or density could be considered as components of an effective competition index.

This study tested candidate components of a competition index based on growth relationships at a fixed seedling age. An operational index should also include a component to assess the ability of a seedling to outgrow the competition over time. Brand and Weetman (1986) proposed a method for estimating seedling free-growth potential based on whether height growth is increasing or decreasing relative to that of the competitors.

Much additional research is needed to develop adequate vegetation-management guidelines for each species and stock type. Such research can use competition indices based on the relevant factors identified in this study.

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